Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE RELATIONSHIPS AND HABITS OF THE MOSASAURS.

THERE is, at present, no group of extinct reptiles which is better known than that of the mosasaurs or pythonomorphs; there is no group concerning whose affinities and relationships there have been more discussion and differences of opinion; and, also, the writer may venture to add, there is no group of extinct vertebrates concerning whose phylogeny and taxonomic position there is now less ground for dispute. The mosasaurs are specialized aquatic lizards, descended from the immediate ancestors of the modern monitors, through the extinct aigialosaurs, and which became wholly extinct near the close of Cretaceous time. They belong among the Lacertilio and are more nearly related structurally and phylogenetically to the living monitors than are the monitors to the living amphisbaenas or chameleons.

Whether the Squamata are an order, as is usually taught in text-books, a superorder, as Fürbringer and Osborn suggest, or a subclass, as Gadow believes, scarcely affects the relations of their component parts, nor the value of the group as a whole, if all the other so-called orders of reptiles are raised to equal rank. But to make the Squamata a superorder, as does Osborn in a recent publication,[1] while leaving far more specialized groups, such as the pterodactyls or turtles, in their former ordinal positions, is manifestly inconsistent. I know not what may be the object of taxonomy unless to indicate the relative degrees of divergence or of specialization of organisms; and to separate the scaled reptiles from the Rhynchocephalia by superordinal characters, while the far greater differences between the pterodactyls and other reptiles, for instance, are accorded an ordinal value only, is, in my opinion, unjustifiable. Nor can it be said that the differences between a lizard and a snake have nearly as much value as those between any other two groups of reptiles properly called orders.

---

[1] *Memoirs of the American Museum of Natural History*, Vol. I (N. 1903), p. 456.

That the classification of the vertebrates will some time reach a fairly satisfactory stability is certain, but that this much-wished-for consummation is not at the present time a reality is painfully evident. Especially is the lack of a taxonomic equilibrium between the various groups of reptiles and those of the birds very apparent. In every group of organisms, where individuals and species are abundant, there is a constant, an almost unchecked, tendency to raise the lower divisions to a higher rank, without due regard to their relative values, so far as those of other groups are concerned; and this tendency will never be discouraged save by the general morphologist; the specialist usually lacks that breadth of view so necessary for a proper perspective. The ornithologists, especially, have been in the past a law unto themselves in this respect, without due fear of the results of their taxonomic misdeeds before their eyes. Twenty-five or thirty groups of birds have been given ordinal rank, while it seems evident that the whole class scarcely presents as many or as wide internal differences, unless it be in a few forms, as are found in not a few single groups of reptiles that are usually called orders. But, I respectfully submit, the raising of the orders of reptiles to subclass rank, as Gadow has done, is not the proper solution of this difficulty. Unless we invent superclasses and superkingdoms, or some entirely new classificatory denominations, an impassable wall will soon be reached, when all the orders are leveled up to subclasses, and we are no nearer a final symmetrical classification than we were, though there may have been many excellent opportunities for coining new names.

The relationship of the mosasaurs to certain modern lizards, the Varanidae, was pointed out by Cuvier in his original description of the famous Maestrichtian example one hundred years ago. Goldfuss, Owen, and Marsh all recognized this relationship as a real one, and refused to give to these animals the rank which Cope insisted upon giving. It was Baur, however, who first strongly emphasized the importance of their varanid affinities. He gave to the mosasaurs only a family rank in the superfamily Varanoidea; perhaps an extreme view, but one which more recent discoveries have, I believe, in large measure substantiated. Gadow, very recently, has gone to the opposite extreme in separating the mosasaurs into a distinct subclass away from the subclass Squamata. Cope, notwithstanding his wide acquaintance with living and fossil reptiles, urged that their ophidian affinities were stronger than their lacertilian ones. Baur believed them to be only specialized and modified varanids; while Osborn has failed to see any marked varanid affinities in them, even suggesting that they did not arise from the same common stem.

In 1892 Kramberger-Gorjanović[1] described from the Lower Cretaceous (probably Gault) of the island Lesina, near the Dalmatian shores of the Adriatic, the remains of a remarkable lizard, which he called *Aigialosaurus*. While his figures have recently been shown to be incorrect in some details, and while some of his minor interpretations were manifestly wrong, he correctly assigned to his new genus and its allies an intermediate position between the true Varanidae and the Mosasauridae, suggesting that they had descended from the Varanidae and were ancestral to the Mosasauria, while from them had been derived the dolichosaurs as a side branch.

> Aus unseren Betrachtungen aber folgt ganz unzweideutig, dass man die erwähnten fossilen Gattungen weder der Familie Varanidae, noch direkt den Pythonomorpha zutheilen kann. Sie sind einergemassen Collectivtypen, welche an sich Merkmale zweier Unterordungen u. zw. der Lacertilia und Pythonomorpha tragen, ... eine Uebergangsgruppe zwischen die Unterordnungen Lacertilia und Pythonomorpha zu stellen ist.

His conclusions regarding the relationships of the Mosasauria are the more creditable from the fact that the only information available to him at that time concerning them was incomplete, and in part erroneous. Nevertheless, so apparent were they that both Boulenger and Dollo accepted them, recognizing in *Aigialosaurus* an ancestral type.

More recently, Kornhuber[2] has described and figured, in an excellent way, the remains of another lizard from Lesina, closely allied to *Aigialosaurus*. So evident were the relationships of his *Opetiosaurus* to *Varanus* that he was inclined at first to unite them in the same genus. Unfortunately Kornhuber was apparently ignorant of the recent publications by Merriam, Osborn, and the writer upon the mosasaurs. Had he been more familiar with the structure of the mosasaurs, I doubt not that he would have recognized more clearly their relationships, and would have detected certain wrong determinations, clearly apparent in his figures, and recognized by Nopcsa—the supraorbital, nasals, columella, etc. There is no supraorbital in the mosasaur skull.

---

[1] "Rad" der südslavischen Akademie der Wissenschaften und Kunst (Agram), Vol. CIX, pp. 96–123; Plate I, ff. 1, 2; Plate II, ff. 1, 2, 4.

[2] *Abhandlungen der k.-k. geologischen Reichs-Anstalt zu Wien*, 1901.

To Nopcsa,[1] very recently, is due the credit for correctly estimating the value of the various annectant characters in these and the other known Cretaceous lizards. His views, though only amplifications and confirmations of those held by other writers, are supported by such undeniably forceful arguments that they cannot be gainsaid.

Aigialosaurus and *Opetiosaurus* especially, with other Lower Cretaceous lacertilians, were clearly in a direct ancestral line between the mosasaurs and the undoubted direct ancestors of the modern monitors, thus confirming Baur's views and disproving those of Osborn. These semi-aquatic lizards lived, evidently in abundance and in many forms, during the latter part of the Lower Cretaceous time, at least in southern Europe. The earliest mosasaurs of which we have any knowledge are probably those from the Cenomanian of New Zealand, and it is not at all improbable that their birthplace was somewhere near the Mediterranean Sea, at or near the close of the Lower Cretaceous. Dollo long ago expressed the opinion that the center of dispersion of the mosasaurs was somewhere in the vicinity of New Zealand, and his views were probably not far wrong. They reached northern Europe shortly after the beginning of the Upper Cretaceous, and North America before the beginning of the Senonian.

Aigialosaurus and *Opetiosaurus* especially—for they are closely allied—so far as the structure of the skull is concerned, present a most striking resemblance to the mosasaurs, save perhaps in the absence of pterygoid teeth. They have the same peculiar form of the quadrate, similar teeth, similar frontal and parietal bones, nares, and, most remarkable of all, the same peculiar hinge in the lower jaws, unknown in other reptiles. Were the vertebræ and ribs to be found in the Kansas chalk unassociated with limb bones, they would almost without hesitation be referred to the mosasaurs. The hands and feet have the same strong resemblances in their form, but there is no hyperphalangy, a character but feebly indicated in some of the mosasaurs. In the elongated limb bones, and especially in the presence of a true sacrum, the real differences between these reptiles are seen. On the other hand, it is especially in those characters wherein they resemble the mosasaurs that they differ from the monitors. Like the mosasaurs, they have but seven vertebræ in the neck, a number found in no other scaled reptiles. It is very certain that they had webbed feet, though the claws had not disappeared.

---

[1] *Beiträge zur Paleontologie und Geologie Oesterreich-Ungarns und des Orients.* Vol. XV (1903), Plates V, VI.

That the varanids are a very old group, dating at least as far back as the Jurassic, seems highly probable, especially so in the light of the recent discovery of an iguanid lizard by Broom in the Karoo beds of South Africa. As was long ago shown by Boulenger, Beddard, and others, the Varanidae are an isolated group among modern lizards, distinguished not only in the structure of their skeleton, but also by many other characteristic differences in their anatomy.

In my opinion, there are no more striking examples of evolution presented in all vertebrate paleontology than that of the aquatic mosasaurs of the Upper Cretaceous, through the semi-aquatic aigialosaurs of the Lower Cretaceous, from the terrestrial varanoids of the lowermost Cretaceous or Upper Jura.

That the snakes originated from the lizards much earlier than we have any definite knowledge would seem very probable. We have no certain evidence of them prior to the latter part of the Upper Cretaceous, that is, the Laramie; but, since it now seems almost certain that at least two distinct phyla of the lizards leading to modern forms had become well differentiated by the close of the Jurassic, or shortly thereafter, it is not at all unreasonable to suppose that the snakes had branched off as early as, or earlier than, the beginning of the Lower Cretaceous.

The relationships of the chief groups of the Squamata may be expressed as follows:

- Order Squamata (Lepidosauria).
  - Suborder Sauria (Lacertilia).
    - Superfamily Platynota.
      - Family Varanidae Gray. Pleistocene—recent.
        - Genus *Varanus* Merrem. India, Australia, Africa.
      - Family Dolichosauridae (Kramb.) Nopcsa. Cretaceous.
        - Genera: *Dolichosaurus* Owen, *Acteosaurus* Meyer, *Pontosaurus* Kramb., *Adriosaurus* Seeley.
      - Family Aigialosauridae (Kramb.) Nopcsa. Lower Cretaceous.
        - Genera: *Aigialosaurus* Kramb., *Carsosaurus* Kornh., *Opetiosaurus* Kornh., *Mesoleptus* Carnalia.
    - Superfamily Mosasauria.
      - Family Mosasauridae Gervais. Upper Cretaceous.
        - Genera: *Mosasaurus* Conyb., *Clidastes* Cope, *Platecarpus* Cope, *Tylosaurus* Marsh, *Baptosaurus* Marsh, *Plioplatecarpus* Dollo. *Hainosaurus* Dollo, *Prognathosaurus* Dollo, *Phosphorosaurus* Dollo, *Brachysaurus* Williston.
    - Superfamily Kionocrania (true lizards). Trias — recent.
    - Superfamily Amphisbaenia. Oligocene — recent.
    - Superfamily Rhiptoglossa (chameleons). Recent.
  - Suborder Serpentes (Ophidia). Laramie Cretaceous — recent.

It is a remarkable fact, for which there has never been any adequate explanation, that the mosasaurs are wholly unknown in the juvenile condition. Altogether, throughout the world, more than three thousand specimens of these animals have been brought to light during the past century, and every one of them, so far as my own knowledge goes—and I have seen many hundreds—and so far as anything that has been published would indicate, is supposed to be of an adult or fairly mature animal. Not a single specimen which can be suspected to be embryonic is known. I hardly think that the same can be said of any other group of extinct aquatic animals. In the Cretaceous of Kansas the young of the plesiosaurs are fairly common, perhaps every third or fourth specimen showing immaturity. I have found them in almost every stage of adolescence, and the embryos have been discovered in Europe. Furthermore, I have often sought in vain for the remains of young mosasaurs in the stomach contents of different animals in the Kansas Cretaceous, and in the bone-beds, which rarely occur in that formation. Under such apparently favorable circumstances as are presented by the chalk deposits of western Kansas, the seemingly entire absence of all remains of young mosasaurs is inexplicable. Half-grown forms do occur, but none that are very young. As I have previously remarked, it is certain that all mosasaurs did not die of old age. Indeed, the many hyperostosial mutilations of antemortem origin indicate only too well the fierce struggles the mosasaurs had with the carnivorous enemies of their own and other kinds.

If the mosasaurs were exclusively marine animals, it would seem almost certain that they were not viviparous, as were the ichthyosaurs, and probably also the plesiosaurs, and as are some modern lizards. As Fraas has remarked concerning the European ichthyosaurs, if one searches carefully, he will find in many Kansas specimens the remains of the skin and stomach contents, but never has there been found anything which has the faintest suggestion of mosasaur embryos. No aquatic reptiles of the present time lay their eggs in the water. The sea snakes are viviparous, or at least all available information concerning them gives viviparous habits. The sea turtles and the crocodiles lay their eggs upon the beaches, the latter guarding their nests and young. Doubtless the crocodiles of the past had the same beach-laying habits, suggesting that they were never inhabitants of the open oceans. The mosasaurs must have been practically helpless upon land; still it is not impossible that they may have frequented the beaches for the deposition of their eggs, though it is highly improbable that they gave any attention or care to either their eggs or their young. That the eggs of the mosasaurs were more numerous than are those of the terrestrial lizards of the present time is not to be supposed. The waters in which the mosasaurs flourished swarmed with highly predaceous fishes, sharks, and plesiosaurs, to say nothing of the hordes of their own kind; and, unless the eggs were very numerous, or unless the young were jealously guarded by the parent, the young reptiles must have stood very little chance in the fierce struggle for existence.

It is, of course, possible that the shallow waters of the bays and estuaries may have afforded sufficient protection for the young mosasaurs, but this is doubtful, in the entire absence of all remains of such animals in marine deposits. It seems more probable that the mosasaurs were brought forth, perhaps alive, in fresh water, that the females ascended the rivers to breed, and that the young remained in such protected places until fairly able to care for themselves. That the mosasaurs, as also the aigialosaurs, were in part denizens of fresh water may be, perhaps, one reason for the great relative abundance of their remains in the deposits of inland or protected seas. Their occurrence in Kansas associated with great numbers of small turtles, pterodactyls, and birds would seem to be fairly good evidence that they were more littoral than pelagic in their habits.

That mosasaur remains have never been found in fresh-water deposits is not at all conclusive in controversion of this hypothesis. We know very little indeed, if anything at all, of the fresh-water life that existed during the times when the mosasaurs flourished. Possibly the Belly River deposits may furnish some evidence bearing on this hypothesis, though I suspect that the mosasaurs had disappeared in America before the time of those deposits.

It will be of interest to record here certain additional facts concerning the structure of the mosasaurs. A most extraordinarily complete specimen, referred to *Holosaurus abruptus* Marsh, discovered by Mr. E. B. Branson in western Kansas the past summer, has a slight emargination of the coracoids, finally and conclusively demonstrating the invalidity of this character in the separation of the genera. The scales of this form, as apparently also of other species of *Platecarpus*, are without carina.

The pubes meet in a perfect symphysis, not as they are always figured in text-books. The ilia were suspended vertically, and the depth of the body posteriorly is greater than the restorations indicate. The upper ends of the ilia were in relation, not with the first of the pygal vertebræ, as I have contended, but with the second or third at least, as Dollo believed. There were more than ninety vertebræ in the tail. The skeleton measured more than twenty feet in length as it lay in the chalk, with nearly every bone in its proper position. The entire skeleton has been brought to the laboratory in chalk slabs, and when it is finally prepared will, I believe, add a number of new facts to our already full knowledge of these remarkable animals.

S. W. WILLISTON.